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Article

A taxonomic revision of fossil freshwater pearl mussels (Bivalvia: Unionoida: Margaritiferidae) from Pliocene and Pleistocene deposits of Southeastern Europe

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Abstract
Margaritiferidae is an ancient freshwater bivalve family originated in the Jurassic in East Asia. Here, we revise several nominal taxa of fossil freshwater pearl mussels that were recovered from the Upper Pliocene and Pleistocene deposits of the Dniester and Prut river valleys. Based on morphological and stratigraphic data, we found that these nominal taxa belong to the genus *Pseudunio* and are junior synonyms of *P. flabellatiformis* (Grigorowitch-Beresowski, 1915). The new synonymy is proposed as follows: *Margaritifera (Pseudunio) moldavica* Chepalyga, 1964 **syn. nov.**, *Margaritifera (Pseudunio) robusta robusta* Chepalyga, 1964 **syn. nov.**, *Margaritifera (Pseudunio) robusta speensis* Chepalyga, 1964 **syn. nov.**, and *Margaritifera (Pseudunio) robusta tirassica* Chepalyga, 1964 **syn. nov.** All these fossil nominal taxa were described based on minor differences in the shell shape and size, hinge structure, and stratigraphic position. Finally, we suggest an updated phylogenetic scheme of the genus *Pseudunio*, which contains five valid species: *P. marocanus* (Pallary, 1918) [Eocene – Recent, Morocco], *P. auricularius* (Spengler, 1793) [Pliocene – Recent, Southern and Western Europe], *P. homsensis* (Lea, 1865) [Pliocene – Recent, Orontes and Nahr al-Kabir basins], *P. flabellatiformis* (Grigorowitch-Beresowski, 1915) **comb. rev.** [Pliocene – Late Pleistocene, paleo-Dniester and paleo-Danube basins, an extinct lineage related to *P. auricularius* and *P. homsensis*], and *P. flabellatus* (Goldfuss, 1837) **comb. rev.** [Miocene, paleo-Danube Basin, a stem lineage, MRCA of *P. auricularius* - *P. homsensis* clade].

Key words: *Pseudunio*, Margaritiferinae, Quaternary, paleo-Danube Basin, paleo-Dniester Basin, Black Sea, Moldova.

Introduction

Numerous fossil nominal taxa of freshwater pearl mussels (Bivalvia: Unionoida: Margaritiferidae) were introduced by paleontologists based on the differences in shell shape, size, umbo position, shape of adductor scars, and hinge structure (Bogatchev, 1961; Chepalyga, 1964, 1965, 1967; Devyatkin et al., 1971). However, recent advances in phylogenetic and phylogenomic modeling (Bolotov et al., 2016; Araujo et al., 2017; Lopes-Lima et al., 2018) indicate that these mussels share slow evolutionary and diversification rates.

Furthermore, studies of recent taxa reveal that freshwater pearl mussels share high levels of intraspecific morphological variability and that minute morphological differences cannot be used as species-level diagnostic characters (Bolotov et al., 2015; Vikhrev et al., 2017; Lopes-Lima et al., 2018). Almost all recent species have strictly allopatric distribution ranges, with the only exception of *Margaritifera middendorffi* (Rosén, 1926) and *M. laevis* (Haas, 1910) having a secondary sympatric zone in the Sakhalin Island, South Kurile Archipelago, and Hokkaido (Bolotov et al., 2015, 2016; Lopes-Lima et al., 2018). In contrast, a description of fossil sympatric taxa is a commonly accepted approach in systematic paleontology, when 2-3 or more closely related species are described from a single locality (Chepalyga, 1964; Devyatkin et al., 1971; Delvene et al., 2016) that may lead to overestimation of the actual diversity of fossil taxa because the sympatric occurrence of closely related species is an unusual phenomenon (Lopes-Lima et al., 2018).

A broad-scale integrative revision of the recent Margaritiferidae (Lopes-Lima et al., 2018) reveals that this family contains two subfamilies (Margaritiferinae Henderson, 1929 and Gibbosulinae Bogan, Bolotov, Froufe & Lopes-Lima, 2018), four genera (*Margaritifera* Schumacher, 1815, *Pseudunio* Haas, 1910, *Cumberlandia* Ortmann, 1912, and *Gibbosula* Simpson, 1900), and 16 species. The thick-shelled margaritiferids from the Mediterranean Region and Morocco were placed in the genus *Pseudunio*, with three recent species: *P. auricularius* (Spengler, 1793), *P. homsensis* (Lea, 1865), and *P. marocanus* (Pallary, 1918) (Lopes-Lima et al., 2018). However, the phylogenetic position of several fossil taxa related to this genus remains unclear, while paleontologists repeatedly suggested to use *Pseudunio* as generic or subgeneric name for fossil taxa with fully developed dentition, e.g. *Margaritifera flabellata* (Goldfuss, 1837) and *M. flabellatiformis* (Grigorowitch-Beresowski, 1915) (Scholz et al., 2007; Schneider and Prieto, 2011). Nesemann (1993) has already placed these fossil taxa within the genus *Pseudunio*.

This study aims to revise several fossil taxa of Margaritiferidae described from the Pleistocene deposits of the Dniester and Prut river valleys in Moldova (Table 1) and to discuss the speciation in the genus *Pseudunio* using paleontological, biogeographic, and molecular evidences.

Table 1. Stratigraphic range of the European *Pseudunio* taxa after Chepalyga (1965).

Epoch	Division	Nominal taxa (original combinations)
Pleistocene	Upper	*Pseudunio auricularius* (Spengler, 1793)
	Middle	*Margaritifera* (*Pseudunio*) *robusta speensis* Chepalyga, 1964, *M.* (*P.*) *robusta tirassica* Chepalyga, 1964
	Lower	*M. (P.) moldavica* Chepalyga, 1964, *M. (P.) robusta robusta* Chepalyga, 1964
Pliocene	Upper	N/A
	Middle	*P. flabellatiformis* (Grigorowitch-Beresowski, 1915)
	Lower	*P. flabellatus* (Goldfuss, 1837)
Miocene	Upper	*P. flabellatus* (Goldfuss, 1837)

Materials and methods

We were unable to find the type series of *Margaritifera (Pseudunio) moldavica* Chepalyga, 1964, *M. (Pseudunio) robusta robusta* Chepalyga, 1964, *M. (P.) robusta speensis* Chepalyga, 1964, and *M. (P.) robusta tirassica* Chepalyga, 1964 in the collection of the Geological Institute of the Russian Academy of Sciences, Moscow, Russia. We therefore studied the images of the type specimens and the original descriptions (Chepalyga, 1964, 1965). Additionally, a series of complete subfossil *Pseudunio* shells (*N* = 17) has been excavated from an outcrop of the Middle Pleistocene riverine deposits near Sucleia village, paleo-Dniester River valley, Transnistria, Moldova [46.8330° N, 29.6982° E]. The stratigraphic profile of this outcrop is presented in Fig. 1. An ancient riverbed substrate, in which *Pseudunio* shells are deposited, is illustrated in Fig. 2. The Middle Pleistocene age of the outcrop was previously established by Yanshin (1989) and Adamenko (1986). This outcrop is located not far from the Blizhniy Khutor (distance from Sucleia of 9 km N) and Speya (35 km SE) localities, from which four fossil taxa under discussion were described, but it stratigraphically corresponds to the Middle Pleistocene Speya locality. The collected materials are deposited in the collection of the Russian Museum of Biodiversity Hotspots (RMBH thereafter), Federal Center for Integrated Arctic Research, Russian Academy of Sciences, Arkhangelsk, Russia. In summary, known records of the Margaritiferidae from the Pliocene and Pleistocene deposits are mostly concentrated in the paleo-Dniester and paleo-Prut river valleys (Fig. 3). Shells of the recent species *P. auricularius* and *P. homsensis* were studied in the malacological collections of the Senckenberg Research Institute and Natural History Museum, Frankfurt, Germany (SMF), National Museum of Natural History, Madrid, Spain (MNCN), and the RMBH.

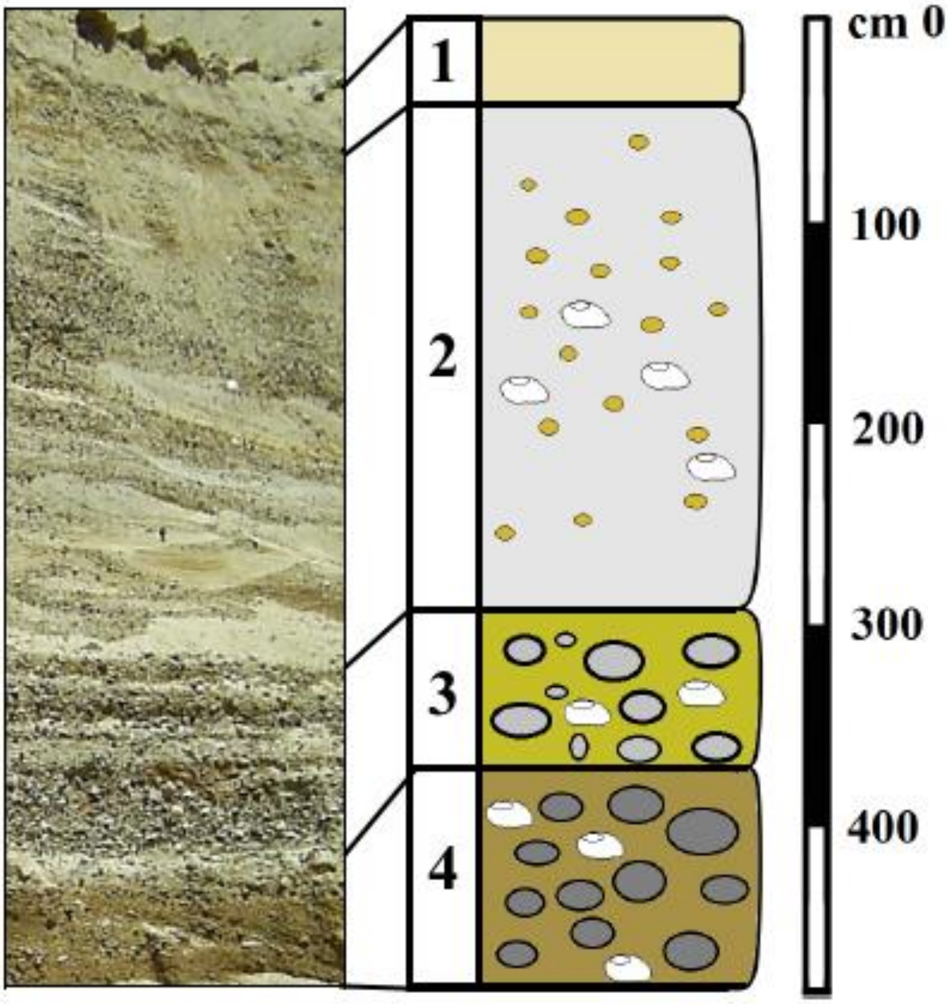

Figure 1. Stratigraphic profile of the Sucleia outcrop, paleo-Dniester River valley, Middle Pleistocene, Moldova. The thickness of outcrop in the studied area is 4.6 m. Layers: (1) 0-40 cm – light-yellow sand with small pebbles; 2) 40-290 cm – light-brown gravel with gray sand and *Pseudunio* shells; 3) 290-370 cm – coarse pebble with sand and numerous *Pseudunio* shells; 4) 370-460 cm – pebble with light-brown sand and *Pseudunio* shells. Photo: Teodor F. Obada.

We applied a comparative morphological analysis with a special focus to the shell shape, structure of the hinge plate, umbo position, and the presence/absence of the shell plication. To estimate conchological differences between samples of fossil taxa, we applied a principal component analysis (PCA) algorithm implemented in PAST v. 3.04 (Hammer et al. 2001) using our shell measurements and published data on the type series (Chepalyga, 1964, 1965). Three shell dimensions for each specimen were measured using a caliper (±0.1 mm): length (L), height (H), and width (W) of the shell, all taken at the maximum diameter.

The distribution map was created using ESRI ArcGIS 10 software (www.esri.com/arcgis); the topographic base of the map was created with ESRI Data and Maps. Reliable localities of fossil and recent taxa were collected from the body of available literature (Bogatchev, 1961; Chepalyga, 1964, 1965, 1967; Vikhrev et al., 2017; Prie et al., 2018).

Figure 2. Subfossil riverbed substrate with a *Pseudunio flabellatiformis* shell, Sucleia outcrop, paleo-Dniester River valley, Middle Pleistocene, Moldova. Scale bar = 100 mm. Photo: Teodor F. Obada.

Results

Morphological patterns. Our sample of subfossil *Pseudunio* shells from the Middle Pleistocene deposits near the Sucleia village can be considered *M.* (*P.*) *robusta speensis* or *M.* (*P.*) *robusta tirassica* based on the stratigraphic position (Figs. 1-4). However, Sucleia's shells are much larger, with the mean length (±s.e.m.) of 114.6±2.0 (range 102.1–128.4) mm, mean height of 64.3±0.9 (range 59.3–72.1) mm, and mean width of 38.2±0.7 (range 33.7–42.5) mm (*N* = 17). These values are within the size ranges proposed for *M. (P.) moldavica* and *M. (P.) robusta robusta* in the original descriptions (Table 2), although there is a significant overlap of the 95% confidence ellipses of almost all nominal taxa based on the PCA scatter plot (Fig. 5). Morphological differences between fossil nominal taxa from Southeastern Europe are presented in Table 2. In summary, they differ from each other by a number of conchological features such as the shell size, shape, thickness, size and shape of the hinge plate, umbo position, and the presence/absence of the shell plication. However, we were unable to find any diagnostic character to distinguish all fossil taxa, *P. auricularius*, and *P. homsensis* from each other by conchological features (Figs. 4, 6-8). The shape of mantle attachment scars varies from round to ovate even within a single specimen (Fig. 9).

Stratigraphic and geographic ranges. All taxa under discussion were described from two localities in the Dniester Valley in Moldova (Table 2). The geographic distance between these localities is 28 km. *M. (P.) moldavica* and *M. (P.) robusta robusta* were introduced from the Lower Pleistocene deposits near the Blizhniy Khutor village, while two other subspecies of *M. (P.) robusta* were described from the Middle Pleistocene deposits near the Speya village.

Species in the genus *Pseudunio*. Based on morphological investigation and available phylogenetic data (Bolotov et al., 2016; Lopes-Lima et al., 2018), this genus includes five species: *P. auricularius*, *P.*

homsensis, *P. marocanus*, *P. flabellatus* **comb. rev.**, and *P. flabellatiformis* **comb. rev.** A brief taxonomic review of all *Pseudunio* species considered valid under this study is presented in Table 3.

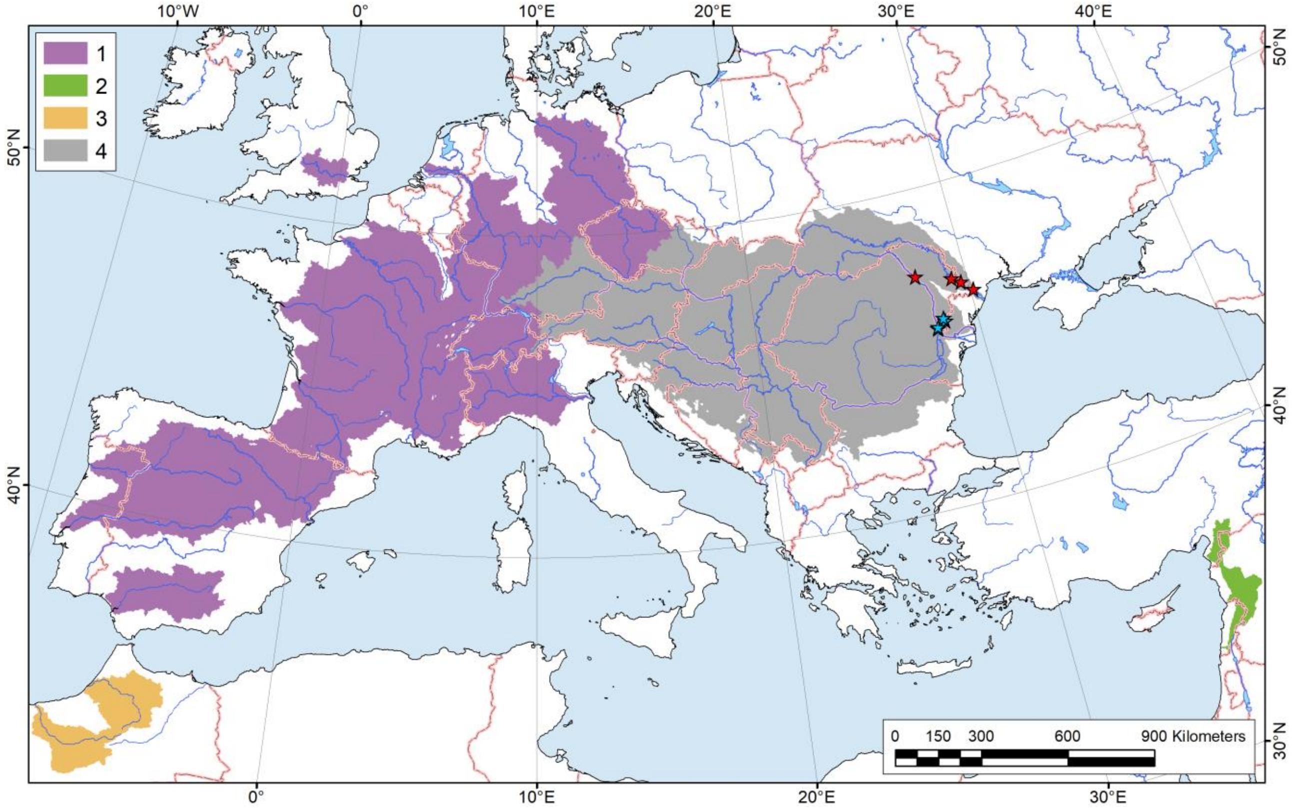

Figure 3. Distribution ranges of *Pseudunio* taxa. The range of each species is illustrated based on the corresponding river drainages: 1 – former range of *P. auricularius* based on fossil and recent records (Araujo and Moreno, 1999; Araujo and Ramos, 2001; Prie et al., 2018); 2 – range of *P. homsensis* based on recent records (Vikhrev et al., 2017); 3 – range of *P. marocanus* based on recent records (Lopes-Lima et al., 2018); 4 – former range of *P. flabellatiformis* with its synonyms (*M. moldavica* **syn. nov.**, *M. robusta robusta* **syn. nov.**, *M. robusta speensis* **syn. nov.**, and *M. robusta tirassica* **syn. nov.**) based on fossil records (Bogatchev, 1961; Chepalyga, 1964, 1965, 1967; Bolotov et al., 2016). Stars indicate records of *P. flabellatiformis* from the Pliocene (blue) and Pleistocene (red) deposits of Southeastern Europe (Bogatchev, 1961; Chepalyga, 1964, 1965, 1967; Bolotov et al., 2016).

Discussion

Taxonomic summary. We found that four nominal taxa, i.e. *M. (P.) moldavica*, *M. (P.) robusta robusta*, *M. (P.) robusta speensis*, and *M. (P.) robusta tirassica* most likely belong to a single fossil species. *M. (P.) moldavica* and *M. (P.) robusta robusta* are represented by large old shells (>100 mm long), while *M. (P.) robusta speensis* and *M. (P.) robusta tirassica* are represented by smaller shells that seem to be younger specimens of the same species (<80 mm long). However, the latter taxa may also be a dwarf ecophenotype associated with unfavorable environmental conditions (Bogatchev, 1961). For example, a tributary of the Missouri River in the Yellowstone National Park is inhabited by a dwarf population of *Margaritifera falcata* (Gould, 1850), which does not have significant molecular differences from other populations of this species, and has likely originated due to strong influence of geothermal waters to the habitat (our unpubl. data). Multiple ecophenotypical varieties were described for *P. flabellatus*, e.g. small-sized specimens from the Berzdorf Basin and lacustrine and riverine morphs from Hungary (Scholz et al., 2007; Schneider and Prieto, 2011). It should be noted that Chepalyga (1964) described *M. (P.) robusta speensis* and *M. (P.) robusta tirassica* from the same locality and deposit (Table 2) that does not correspond to the traditional concept of subspecies precluding the delineation of two sympatric subspecies (subspecies must be allopatric by definition).

Table 2. Types, type localities, ranges and differential diagnoses of fossil nominal *Pseudunio* taxa from Southeastern Europe (after Chepalyga, 1964, 1965).

Taxon (original combination)	**Type and type locality**	**Stratigraphic and geographic range**	**Shell length range (mm)**	**Original differential diagnosis**
Margaritifera (Pseudunio) moldavica Chepalyga, 1964	Holotype GIN M8/63*: Dniester Valley, Blizhniy Khutor, near Tiraspol, Lower Quaternary deposits [46.9072° N, 29.6544° E]	Lower Quaternary of Moldova, Dniester and Prut valleys (5th terrace)	105–149	Distinguished from *P. auricularius* by a more pronounced umbo displaced forward, more massive teeth, very broad hinge plate, and less curved shell; from *P. marocanus* by a larger size, umbo displaced further forward, and more massive teeth; from *M. redomica* [=*P. marocanus*] by a more elongate shell shape, low umbo displaced towards the anterior end, and shape of muscle scars; from *P. flabellatiformis* by a more pronounced umbo, thicker hinge plate, and the lack of shell plication
M. (P.) robusta robusta Chepalyga, 1964	Holotype GIN M1/63*: Dniester Valley, Blizhniy Khutor, near Tiraspol, Lower Quaternary deposits [46.9072° N, 29.6544° E]	Lower Quaternary of Moldova, Dniester and Prut valleys (5th terrace)	111–137	Distinguished from *M.* (*P.*) *moldavica* by a higher, shorter shell, more pronounced umbo, more curved lateral teeth; from *M. redomica* [=*P. marocanus*] by a more massive hinge plate and rounded anterior end; from *P. flabellatiformis* by the lack of shell plication, shorter and thicker shell, more pronounced umbo, and more massive hinge plate
M. (*P.*) *robusta speensis* Chepalyga, 1964	Holotype GIN M26/63*: Dniester Valley, Speya, Middle Quaternary deposits [47.0143° N, 29.3192° E]	Middle Quaternary of Moldova, Dniester Valley	63–78	Distinguished from *M.* (*P.*) *robusta robusta* by a smaller size (shell is two times smaller), less pronounced umbo, more convex dorsal margin, and weakly expressed pallial sinus
M. (*P.*) *robusta tirassica* Chepalyga, 1964	Holotype GIN M22/63*: Dniester Valley, Speya, Middle Quaternary deposits [47.0143° N, 29.3192° E]	Middle Quaternary of Moldova, Dniester Valley	63–79	Distinguished from *M.* (*P.*) *robusta speensis* by a thinner shell, less massive teeth, and almost straight dorsal margin; from *M.* (*P.*) *robusta robusta* by a smaller size (shell is two times smaller), oval shell shape, and less curved lateral teeth

*Geological Institute of the Russian Academy of Sciences, Moscow, Russia. Types were not found in this depository (Artem A. Lyubas, pers. obs., 2013).

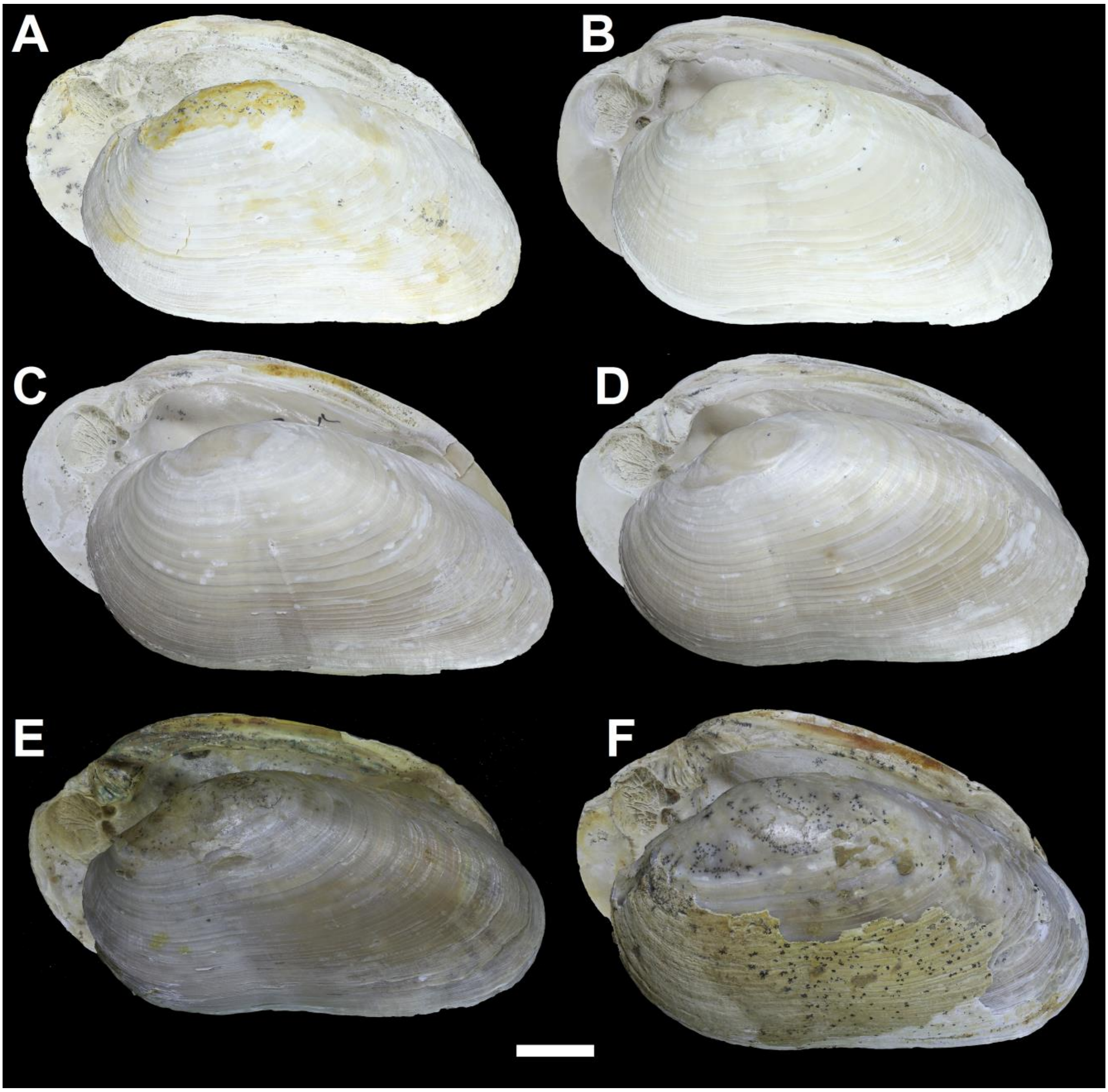

Figure 4. Subfossil shells of *Pseudunio flabellatiformis* (Grigorowitch-Beresowski, 1915) **comb. rev.** from the outcrop of the Middle Pleistocene riverine deposits near Sucleia village, paleo-Dniester River valley, Transnistria, Moldova: **A**) specimen no. 1 (RMBH); **B**) specimen no. Sc1 (RMBH); **C**) specimen no. Sc5 (RMBH); **D**) specimen no. Sc8 (RMBH); **E**) specimen no. Sc12 (RMBH); **F**) specimen no. Sc13 (RMBH). Scale bar = 20 mm. Photos: Artem A. Lyubas.

P. flabellatiformis described from the Upper Pliocene deposits of the Prut Valley near the Slobozia Mare village in Moldova (Grigorowitch-Beresowski, 1915; Bogatchev, 1961) appears to be the oldest available name for the *Pseudunio* species from the Pliocene and Pleistocene of Southeastern Europe. However, Schneider and Prieto (2011) suggested that *Unio pucici* Brusina, 1902 may have priority over the name *P. flabellatiformis*, if these taxa are conspecific. This taxonomic puzzle is beyond the scope of our study and needs further research efforts. However, *Unio pucici* Brusina, 1902 has a strongly ornamented shell (Schneider and Prieto, 2011) that is typical rather for *P. flabellatus* than *P. flabellatiformis*. Nesemann (1993) assumed that *P. flabellatus* (with its synonyms) and *P. flabellatiformis* may represent a single species existing during a long-term period from the Neogene to the Quaternary epoch. In contrast, Schneider and Prieto (2011) considered these taxa to be two separate species, with *P. flabellatus* being an older Miocene lineage, and *P. flabellatiformis* being a younger Pliocene – Pleistocene lineage. This latter hypothesis fully agrees with our results.

Table 3. Taxonomic review of *Pseudunio* species.

Species	Phylogenetic placement	Temporal range	Geographic range	References
P. marocanus (Pallary, 1918)	Terminal (recent) species	Eocene – Recent	Morocco	Araujo et al. (2009); Lopes-Lima et al. (2018)
P. flabellatus (Goldfuss, 1837) **comb. rev.**	Stem lineage, MRCA of *P. auricularius - P. homsensis* clade	Miocene	Western and Eastern Europe: paleo-Danube Basin	Schneider and Prieto (2011); Bolotov et al. (2016); Lopes-Lima et al. (2018)
P. flabellatiformis (Grigorowitch-Beresowski, 1915) **comb. rev.**	Extinct lineage related to *P. auricularius* and *P. homsensis*	Late Miocene – Late Pleistocene	Eastern Europe: Danube and Dniester paleo-basins, Black Sea drainage	Schneider and Prieto (2011); Bolotov et al. (2016); Lopes-Lima et al. (2018)
P. auricularius (Spengler, 1793)	Terminal (recent) species	Late Miocene – Recent	Southern and Western Europe	Lopes-Lima et al. (2018); Prie et al., 2018
P. homsensis (Lea, 1865)	Terminal (recent) species	Late Miocene – Recent	Orontes and Nahr al-Kabir basins in Syria, Turkey and Lebanon	Vikhrev et al. (2017)

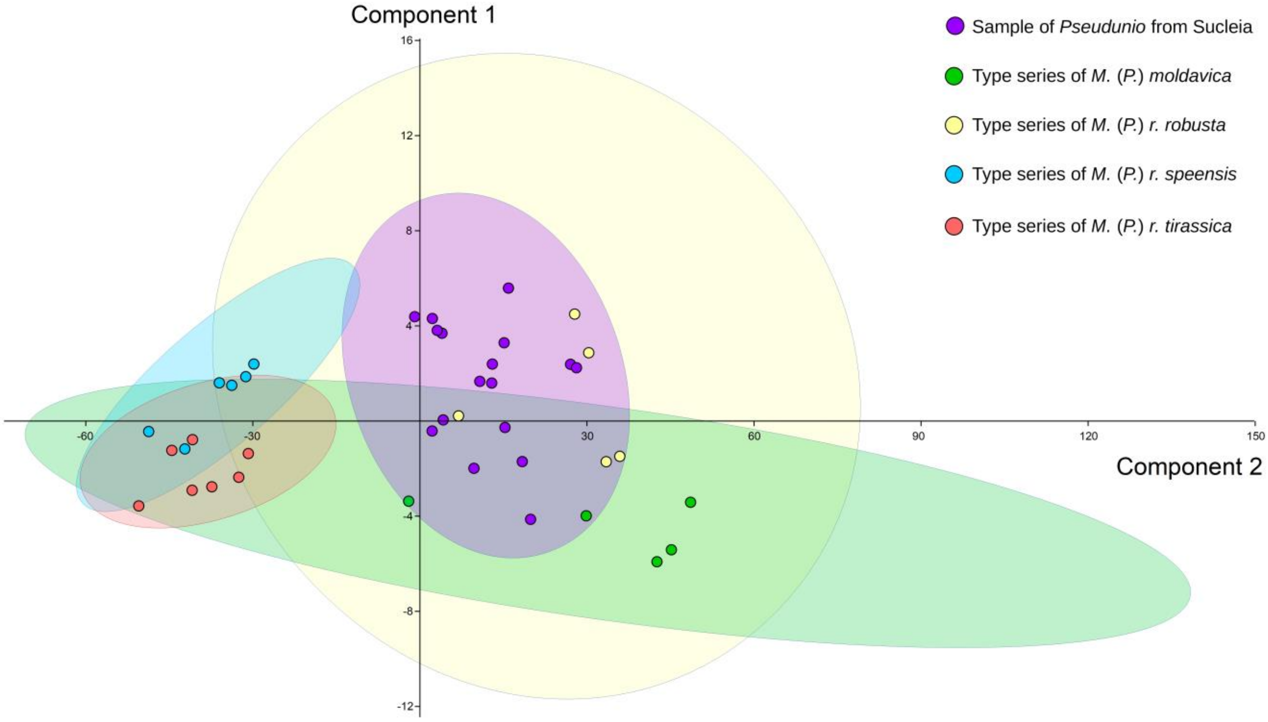

Figure 5. Scatter plot of PCA based on the shell measurements of our *Pseudunio* sample from the Sucleia locality and the type series of fossil nominal taxa from the Speya and Blizhniy Khutor localities (Chepalyga, 1964, 1965). The component 1 and component 2 accounted for 98.8% and 1.0% of the total variance, respectively.

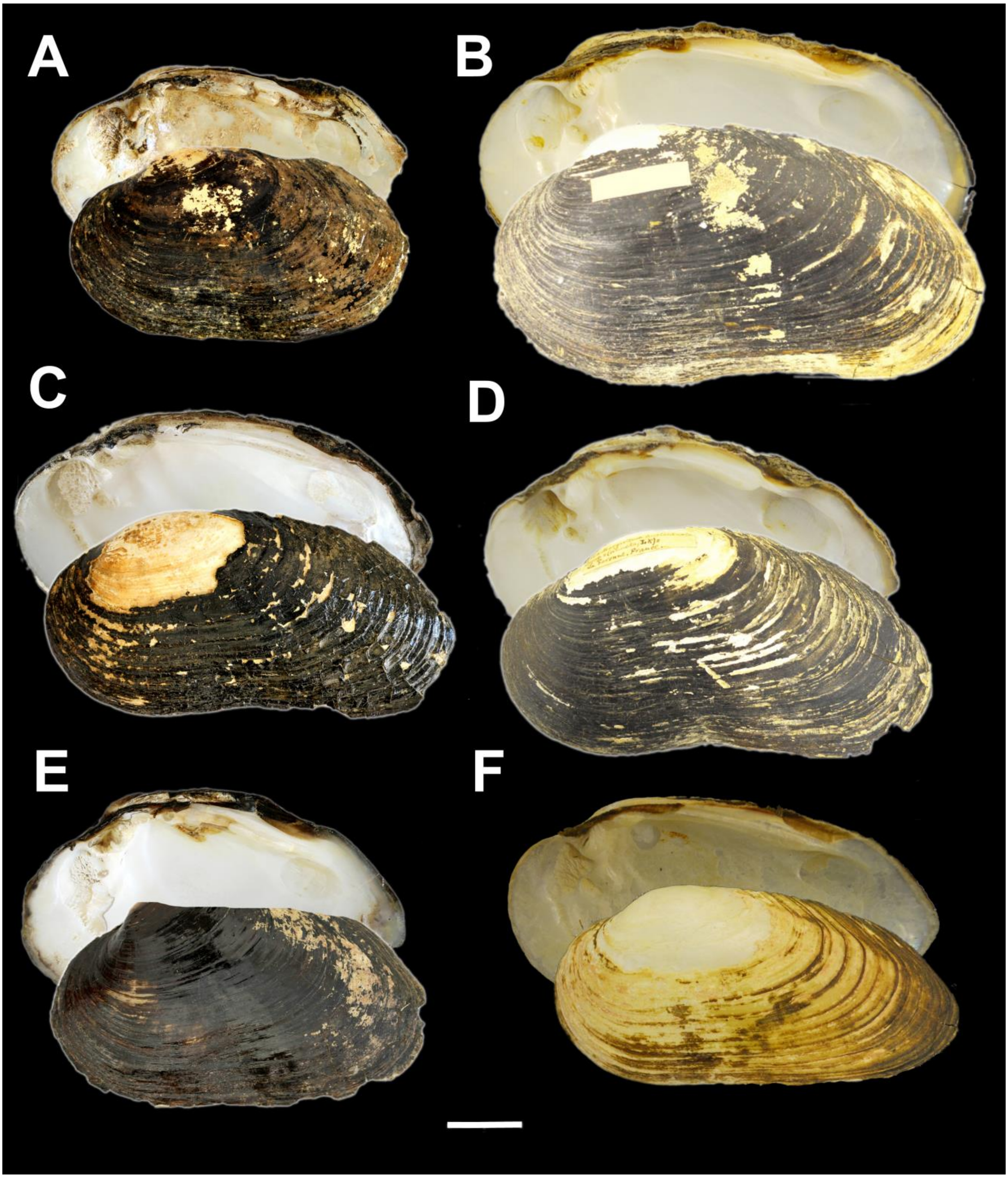

Figure 6. Shells of the recent *Pseudunio auricularius* (Spengler, 1793): **A**) Indre River near Huismes commune, Loire Basin, France (SMF, voucher no. 307623); **B**) Ebro River near Cenicero, La Rioja, Spain (MNCN, voucher no. 15.07/197); **C**) Loire River upstream of Champtoceaux commune, Maine-et-Loire, France (SMF, voucher no. 307850); **D**) Garonne River, France (MNCN, voucher no. 15.07/178); **E**) Indre River near Huismes commune, Loire Basin, France (SMF, voucher no. 307623); **F**) Ebro River near Amposta city, Tarragona, Spain (MNCN, voucher no. 15.07/10366). Scale bar = 20 mm. Photos: Artem A. Lyubas & Ilya V. Vikhrev.

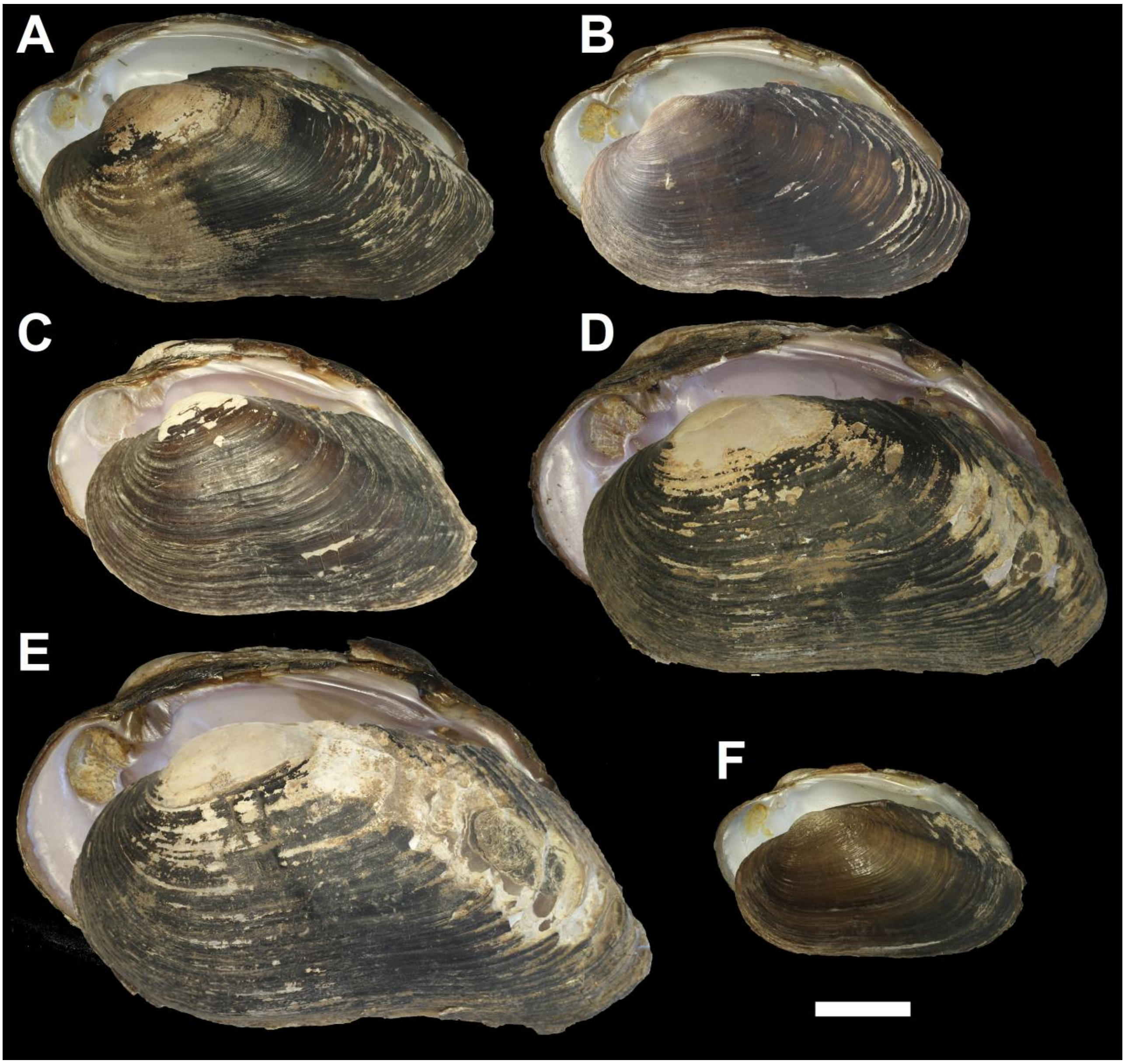

Figure 7. Shells of the recent *Pseudunio homsensis* (Lea, 1865): **A**) Orontes River near Homs, Syria (SMF, voucher no. 4450); **B**) Orontes River near Homs, Syria (SMF, voucher no. 345464); **C**) Orontes River near Homs, Syria (SMF, voucher no. 15263); **D**) Nahr al-Kabir al-Janoubi River near Harida, Syria (SMF, voucher no. 83160) **E**) Nahr al-Kabir al-Janoubi River near Tell Kalat, Syria (SMF, voucher no. 5156); **F**) Orontes River near Homs, Syria (SMF, voucher no. 4548). Scale bar = 20 mm. Photos: Ilya V. Vikhrev.

Preliminary biogeographic scenarios. Based on recent phylogenetic and biogeographic modeling (Lopes-Lima et al., 2018) and paleontological data (Schneider and Prieto, 2011), we suggest an evolutionary scenario for the taxa under discussion as follows (Fig. 10). *P. flabellatus* existed in the paleo-Danube Basin at least since the Early Miocene (Schneider and Prieto, 2011). This species can be considered the most recent common ancestor (MRCA) of a clade that contains *P. flabellatiformis*, *P. auricularius*, and *P. homsensis*. In the Middle Miocene *P. flabellatus* probably expands its range throughout rivers of Southern Europe, Eastern Europe, and the Middle East. Such a broad-scale expansion event via passive dispersal of larvae with fish hosts may have been triggered by a warm and humid period during the Miocene Climatic Optimum (MCO) between 20 and 14 Ma (Böhme, 2003) as it was recently shown for freshwater pond snails, the Lymnaeidae (Aksenova et al., 2018). The extensive development of huge lake systems during the Miocene humid intervals most likely supported successful range expansions of freshwater taxa during this period. For example, vast Middle Miocene freshwater systems were presented in Central and South-Eastern Europe

(Harzhauser and Mandic, 2008), Middle East (Alqudah et al., 2019), and other regions. The MCO ended between 14.0 and 13.5 Ma, with subsequent cool and dry climatic episode leading to an enhanced aridification in Eurasia with disappearance of the Miocene lake complexes (Arenas and Pardo, 1999). This dating corresponds well to the most likely time of separation of *P. auricularius* and *P. homsensis* (mean age = 12.2 Ma, see Fig. 10) inferred by a fossil-calibrated modeling approach (Lopes-Lima et al. 2018). We assume that a broad range of *P. flabellatus* was separated since the end of the MCO into several isolated fragments with subsequent speciation, i.e. the Black Sea Region (*P. flabellatiformis*), Southern Europe (*P. auricularius*), and the Middle East (*P. homsensis*). However, there is another scenario that the populations in the Black Sea Region were connected with those in Southern Europe or the Middle East by the gene flows via migrations of fish hosts, sturgeons that were continuously distributed in coastal basins in these areas at least since the Early Pliocene (Araujo and Ramos, 2001; Kovalchuk et al., 2015). If so, *P. flabellatiformis* may actually be an extinct population of *P. auricularius* or *P. homsensis*, while the lack of clear morphological differences between *P. flabellatiformis* and its two recent allies precludes any final solution on this issue.

Fossil Margaritiferidae with reduced lateral teeth from Southeastern Europe. *Margaritifera* (s. str.) *arca* Chepalyga, 1964 is another nominal taxon that was described from the paleo-Dniester Valley. This species was found in the Upper Pliocene deposits and differs from *Pseudunio* taxa by the lack of lateral teeth (Chepalyga, 1964, 1965, 1967). Additional records of this taxon are known from the Early Pleistocene deposits of the Kuban River delta (Shchelinsky et al., 2016). This species may represent a stem lineage of *Margaritifera margaritifera* (Linnaeus, 1758) (Chepalyga, 1964, 1965, 1967; Bolotov et al., 2016).

Taxonomy

Family Margaritiferidae Henderson, 1929 (Ortmann, 1910)

Subfamily Margaritiferinae Henderson, 1929

Genus *Pseudunio* Haas, 1910
Type species: *Unio sinuata* Lamarck, 1819 [=*Unio auricularius* Spengler, 1793]

Pseudunio flabellatiformis (Grigorowitch-Beresowski, 1915) **comb. rev.**
Unio flabellatiformis Grigorowitch-Beresowski (1915).
Unio flabellatiformis var. *levata* Bogatchev (1961): 229, plate XXIX, figs. 3-4.
Margaritifera (*Pseudunio*) *moldavica* Chepalyga (1964): 38, plate IV, fig. 1.
Margaritifera (*Pseudunio*) *robusta* Chepalyga (1964): 40.
Margaritifera (*Pseudunio*) *robusta robusta* Chepalyga (1964): 42, plate III, fig. 1.
Margaritifera (*Pseudunio*) *robusta speensis* Chepalyga (1964): 42, fig. 1б.
Margaritifera (*Pseudunio*) *robusta tirassica* Chepalyga (1964): 43, plate IV, fig. 2.
Figs. 4, 8C, 9

Types. Whereabouts unknown.

Type strata and locality. Upper Pliocene, Prut River valley near Slobozia Mare village, Danube Basin, Moldova [45.6067° N, 28.1656° E].

Differential diagnosis. This species is conchologically similar to *P. auricularius* and *P. homsensis* (Figs. 4-8). Moreover, clear conchological features to distinguish the recent *Pseudunio* taxa from each other are lacking (Araujo et al., 2009; Lopes-Lima et al., 2018). *P. flabellatiformis* and the recent *Pseudunio* species clearly differs from *P. flabellatus* by the lack of strong corrugate plication of the shell, although a weakly developed plication can be found in some specimens (Chepalyga, 1967; Bolotov et al. 2016; Vikhrev et al. 2017; Lopes-Lima et al., 2018).

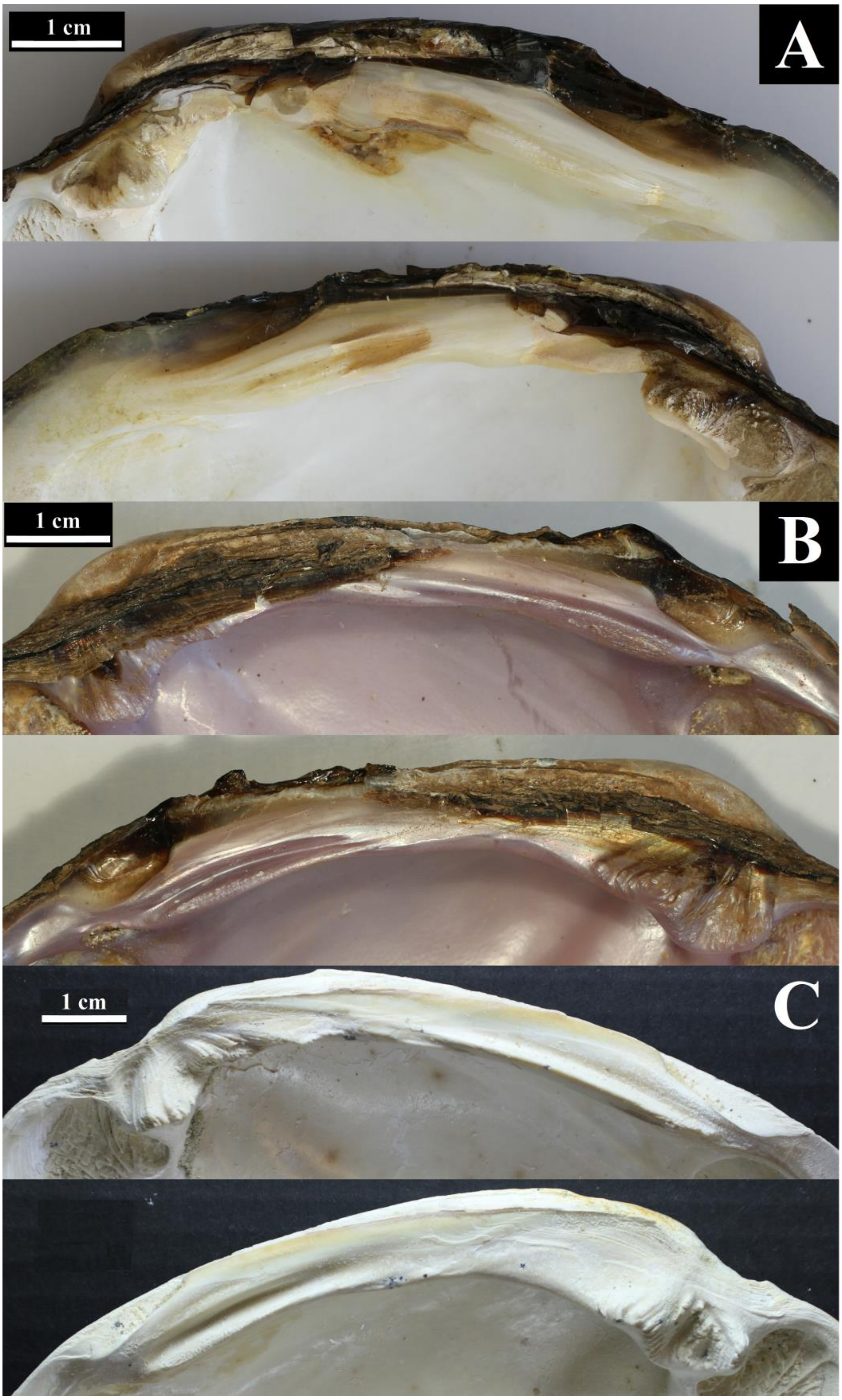

Figure 8. Teeth morphology of recent and fossil *Pseudunio* taxa: **A**) *P. auricularius* from the Indre River near Huismes commune, Loire Basin, France (SMF, voucher no. 307623); **B**) *P. homsensis* from the Nahr al-Kabir al-Janoubi River near Harida, Syria (SMF, voucher no. 83160); **C**) *P. flabellatiformis* **comb. rev.** from the Sucleia outcrop, paleo-Dniester River valley, Middle Pleistocene, Moldova (RMBH, voucher no. Sc1). Scale bars = 10 mm. Photos: Artem A. Lyubas and Ilya V. Vikhrev.

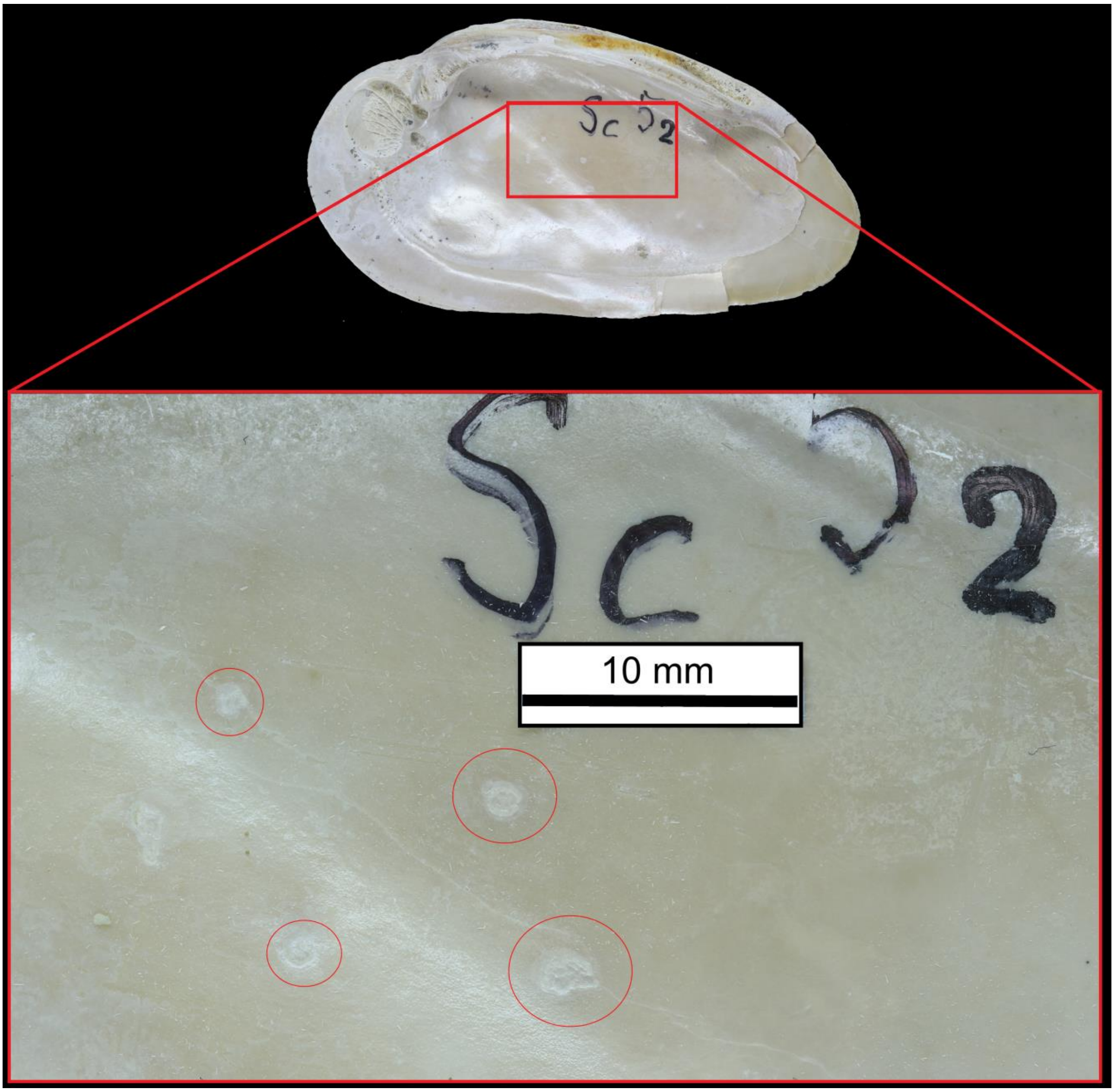

Figure 9. Mantle attachment scars on the inner side of subfossil shell of *Pseudunio flabellatiformis* **comb. rev.** from the Sucleia outcrop, paleo-Dniester River valley, Middle Pleistocene, Moldova (RMBH, voucher no. Sc5). Scale bar = 10 mm. Photo: Artem A. Lyubas.

Phylogenetic position. Extinct lineage related to *P. auricularius* and *P. homsensis*. We assume that this extinct species was originated in a distinct isolate (Danube and Dniester paleo-basins) simultaneously with the two terminal species (*P. auricularius* in Southern Europe and *P. homsensis* in Orontes Basin) since the Middle Miocene.

Stratigraphic and geographic range. Late Miocene – Late Pleistocene, Danube and Dniester paleo-basins, Black Sea drainage, Eastern Europe.

Paleoenvironment. Available data (Chepalyga, 1964, 1965, 1967; this study) indicates that *P. flabellatiformis* inhabited the main channels of large rivers with sandy-gravel and sandy-pebble bottom substrate (Fig. 2). It often co-occurred with *Unio crassus* Retzius, 1788 (or its stem lineages).

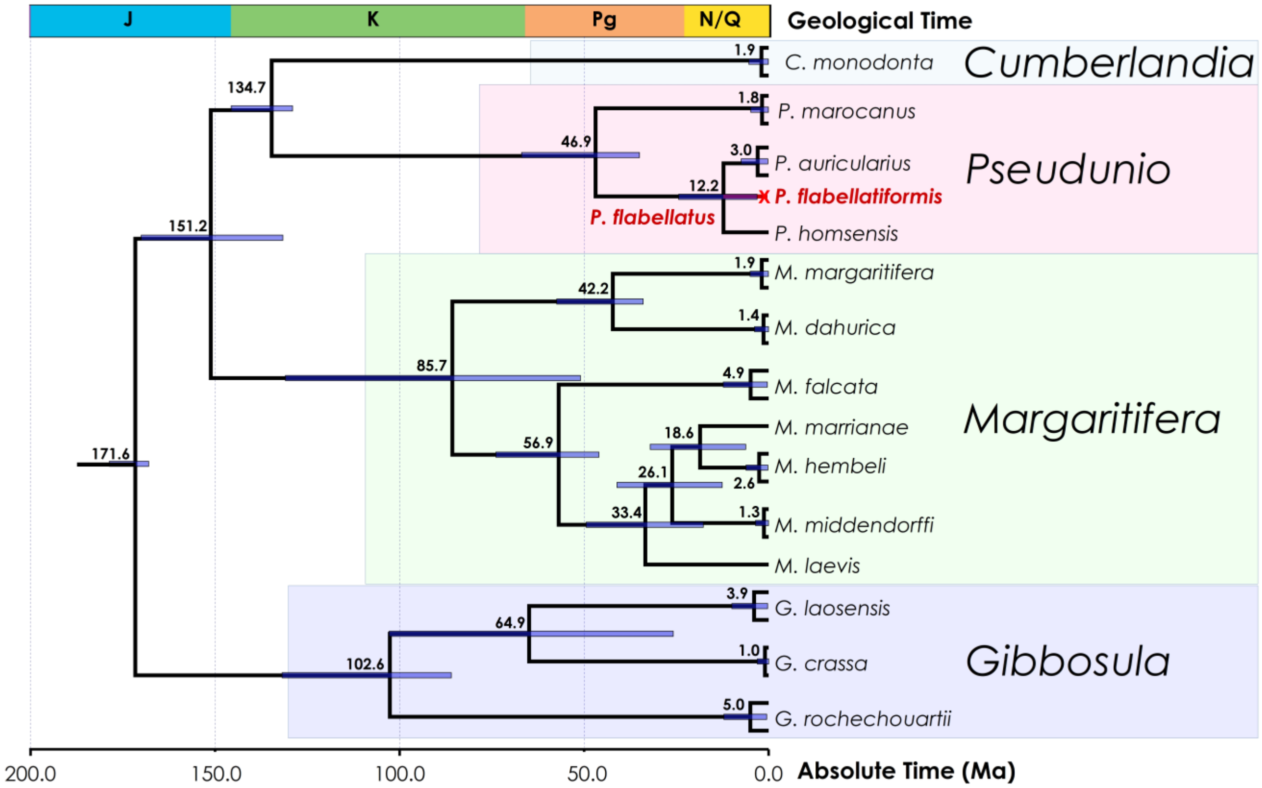

Figure 10. Fossil-calibrated multi-locus ultrametric chronogram of the Margaritiferidae (after Lopes-Lima et al. (2018) with our additions). Bars indicate 95% confidence intervals of the estimated divergence times between lineages (Ma). Black numbers near nodes are mean ages (Ma). Stratigraphic chart according to the International Commission on Stratigraphy, 2015. Fossil species under discussion are in red. We illustrated a putative phylogenetic placement of fossil species, i.e. *Pseudunio flabellatus* (Goldfuss, 1837) **comb. rev.** as a stem lineage (MRCA of *P. auricularius* - *P. homsensis* clade) and *P. flabellatiformis* (Grigorowitch-Beresowski, 1915) **comb. rev.** as an extinct lineage (red branch with X-shaped terminal mark indicating an extinction event in the Late Pleistocene) related to *P. auricularius* and *P. homsensis*.

Pseudunio flabellatus (Goldfuss, 1837) **comb. rev.**
Unio flabellatus Goldfuss (1837): 182.

Types. Lectotype and paralectotype STIPB-Goldfuß-822, Steinmann Institute for Mineralogy, Geology and Palaeontology (formerly Goldfuss Museum), University of Bonn, Bonn, Germany (Schneider and Prieto, 2011).

Type strata and locality. Upper Freshwater Molasse (Middle Miocene), Käpfnach, southern shore of Lake Zürich, Switzerland [approx. 47.2546° N, 8.6160° E] (Schneider and Prieto, 2011).

Differential diagnosis. This species differs from the other *Pseudunio* taxa by a strong corrugate plication of the shell. Furthermore, it seems to be the most ancient lineage among European *Pseudunio* (Schneider and Prieto, 2011).

Phylogenetic position. This species appears to be a stem lineage and the MRCA of a clade that contains the terminal species *P. auricularius* and *P. homsensis*, and the extinct species *P. flabellatiformis*.

Stratigraphic and geographic range. Miocene, Danube Paleo-Basin, Black Sea drainage, Western and Eastern Europe.

Paleoenvironment. This species is known from a variety of riverine and lacustrine paleo-environments (Nesemann, 1993; Scholz et al., 2007; Schneider and Prieto, 2011).

Taxonomic comments. Schneider and Prieto (2011) provided a full redescription of this taxon with a nearly complete list of synonyms.

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